

Functional significance of EEG beta-band oscillations in multisensory perception and selective attention

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1. Summary

1.1. Summary in English

Oscillations are a ubiquitous phenomenon in neural activity. They are found at various spatial scales from single neuron activity over multi-unit responses to large-scale fluctuations, as reflected in local field potentials. A special functional relevance has been attributed to oscillatory synchronization of pre- and postsynaptic cells, which is thought to underlie basic communication and integration mechanisms within and between distinct groups of neurons. Recently, there has been an increasing interest in oscillatory beta band activity (BBA, 13-30 Hz). While traditionally associated with sensorimotor behaviour, research now becomes aware of its putative role in selective attention and large-scale neural communication. The present thesis investigated the functional significance of BBA in a broad range of cognitive tasks, using non-invasive electroencephalography (EEG) measures. **Study 1** examined the influence of simultaneous visual input on the processing of pain, which is known to engage a widely distributed cortical network. The study showed that sensorimotor BBA reflects the strengths of multisensory processing between visual and pain stimuli. Moreover, the study demonstrates that these interactions are inversely related to the strength of painful stimuli. In **Study 2**, auditory speech localization and discrimination was examined in patients with bilateral cochlear implants. This group of individuals is known to have difficulties in speech localization, which might derive from a prior degeneration of auditory pathways. The study demonstrates a lower behavioural performance and stronger medio-central BBA suppression during speech localization in cochlear implant users compared to normal hearing individuals. This suggests that BBA reflects selective spatial attention to auditory speech stimuli. Finally, **study 3** investigated the processes of intersensory attention and temporal orienting in a multisensory cue-target paradigm. The study showed that modulations of anticipatory BBA reflect intersensory attention as well as temporal orienting. Interestingly the results did not reveal interactions between the two mechanisms, suggesting that intersensory attention and temporal orienting can operate largely independent of each other. Taken together, the data from the three studies of this thesis are in line with recent frameworks on the role of BBA in integrative processing and selective attention. Importantly, the studies of this thesis extend previous research by demonstrating the crucial role of BBA in multisensory processing (**Study 1**), selective attention (**Study 2**) and intersensory attention as well as temporal orienting (**Study 3**). The studies also emphasize the high relevance of future research in this field, which will help to further uncover the significance of BBA in sensorimotor, attentional, and integrative functions.

1.2. Summary in German (Zusammenfassung auf Deutsch)

Oszillationen sind ein allgegenwärtiges Phänomen neuronaler Aktivität, welches von Aktionspotentialen einzelner Zellen bis zu großflächigen Fluktuationen lokaler Feldpotentiale reicht. Eine besondere funktionelle Relevanz wird dabei oszillatorischer Synchronisation von pre- und postsynaptischen Zellen zugeschrieben, welche vermutlich maßgeblich an der Kommunikation sowohl innerhalb als auch zwischen neuronalen Ensembles beteiligt ist. In den vergangenen Jahren hat das Interesse an Oszillationen im Beta Band (13-30 Hz) stark zugenommen. Wurden diese ursprünglich vor allem mit motorischen und somatosensorischen Prozessen assoziiert, so schreibt man ihnen mittlerweile komplexe Funktionen in selektiver Aufmerksamkeit und neuronaler Integration zu. Die vorliegende Arbeit hat mittels noninvasiver Elektroenzephalographie die Rolle von Beta-Band Aktivität (BBA) bei einer Reihe unterschiedlicher kognitiver Aufgaben untersucht.

Studie 1 hat sich mit dem Einfluss visueller Reize auf die Verarbeitung von gleichzeitig präsentierten Schmerzreizen beschäftigt, ein Prozess der sich auf weitverzweigte kortikale Netzwerke erstreckt. Als Ergebnis zeigt sich, dass BBA in sensomotorischen Arealen das Ausmaß an Integration zwischen visuellen Reizen und Schmerzreizen widerspiegelt. Die Stärke der Integration ist darüber hinaus invers proportional zur Stärke der Schmerzreize.

Studie 2 hat die Lokalisation und Diskrimination von Sprachlauten bei Patienten mit beidseitigem Cochlear Implantat (CI) untersucht. Diese Personen haben erfahrungsgemäß Schwierigkeiten bei der Lokalisation von Sprache, was auf eine vorhergehende Degeneration von kortikalen auditorischen Pfaden zurückzuführen sein könnte. Die Studie zeigt eine geringere Verhaltensleistung sowie stärkere Modulation medio-zentraler BBA während Sprachlokalisation bei Personen mit beidseitigem CI im Vergleich zu normalhörenden Personen. Dies lässt auf einen Zusammenhang zwischen BBA und Verarbeitungsaufwand sowie selektiver räumlicher Aufmerksamkeit für auditorische Reize schließen. In **Studie 3** wurde das Verhältnis zwischen intersensorischer Aufmerksamkeit und zeitlicher Orientierung im Rahmen eines multisensorischen cue-target Paradigmas untersucht. Als Ergebnis findet sich dass die Modulation antizipatorischer BBA unabhängig voneinander sowohl intersensorische Aufmerksamkeit als auch zeitliche Orientierung reflektiert. Interessanterweise fand sich keine Interaktion zwischen den jeweiligen BBA Antworten, was dafür spricht dass die beiden Aufmerksamkeitsprozesse unabhängig voneinander ablaufen.

Zusammenfassend lässt sich sagen, dass die Ergebnisse der hier vorgestellten Studien im Einklang mit den jüngst aufgestellten Theorien zur Rolle von BBA während kortikaler Integration und selektiver Aufmerksamkeit stehen. Sie erweitern bisherige Forschungsergebnisse, indem sie die Beteiligung von BBA während multisensorischer Verarbeitung (**Studie 1**), selektiver auditorischer Aufmerksamkeit (**Studie 2**), sowie intersensorischer Aufmerksamkeit und zeitlicher Orientierung (**Studie 3**) zeigen. Die Arbeiten unterstreichen zugleich die Bedeutung zukünftiger Forschung in diesem Feld, welche zu einem tieferen Verständnis von BBA im Rahmen von sensomotorischen Prozessen, Aufmerksamkeit und kortikaler Integration führen werden.

2. Neural Oscillations

2.1. Introduction

Today, it is firmly established that oscillatory activity plays a key role in local and long range neural communication and information processing (Engel and Singer, 2001; Fries, 2005; Siegel et al., 2012). Neural oscillations have been observed in a multitude of processes, such as perception (Keil et al., 1999), selective attention (Bauer et al., 2012), working memory (Klimesch et al., 2006), long term memory encoding and retrieval (Damasio, 1990; Herrmann et al., 2004), conscious awareness (Fries et al., 1997), decision making (Donner et al., 2009), multisensory integration (Senkowski et al. 2008), and motor output (Neuper et al., 2006). Apart from their well-documented involvement in physiological processes in healthy individuals, disturbances in neural oscillations have been associated with a number of pathophysiological conditions, such as schizophrenia (Uhlhaas and Singer, 2010), autism (Lai et al., 2010), and Parkinson's disease (Brown, 2006). Further, oscillatory neural activity can be recorded from structures of various orders of magnitude, using a wide range of methodological approaches. For instance, neural oscillations have been observed in spiking behaviour and postsynaptic potentials of single neurons (Llinás and Yarom, 1986; Cardin et al., 2009), in multiunit and local field potential activity in animals (Lakatos et al., 2005; Kreuz et al., 2007), and as a macroscopic measure of local field potential (LFP) activity in electroencephalographic (EEG) and magnetoencephalographic (MEG) recordings in humans (Donner et al., 2009; Hipp et al., 2011). As the three original works of this thesis comprise electrical neural oscillations recorded with the EEG, the focus for the remainder of this thesis will be on oscillations in neural mass activity, as measured with EEG and MEG and, to some extent, intracranial recordings of multi-unit and LFP activity.

In my dissertation, I investigated oscillatory neural activity in the beta band, which comprises frequencies from 13-30 Hz. For a long time, beta-band activity (BBA) has been almost exclusively associated with sensorimotor processes (Kilavik et al., 2013). Only recently, research has begun to uncover the involvement of BBA in a number of higher cognitive processes, such as multisensory integration, selective attention, and temporal orienting (Donner and Siegel, 2011; Arnal, 2012). The studies of my dissertation confirm and extend the recently proposed functional significance of BBA in higher cognitive processes in a number of ways. In the following sections, I will first introduce the five major frequency

bands present in neural oscillations and discuss two influential theories on the functional role of oscillatory activity (Chapter 2.2). Next, I will provide an overview on the functional role of BBA, considering both traditional and more recent views (Chapter 3). I will then give a short summary on the background and findings of the three studies of the present thesis (chapter 4). Finally, I will discuss the results of my studies in relation to the theories and studies introduced in the first four chapters (Chapter 5).

2.2. Oscillatory phenomena observed in local field potentials

Oscillatory neural activity typically governs a set of characteristic frequency bands, which comprise the delta band (0.5-3 Hz), theta band, alpha band (8-12 Hz), beta band (13-30 Hz), and gamma band (> 30 Hz). Research has tried to link each of these frequencies to a number of cognitive processes (see e.g. Buzsáki, 2006). For a long time, delta-band oscillations have been primarily associated with slow wave sleep (Basar et al., 2000), but have more recently also been found during motivational and reward processing (Knyazev, 2007). Moreover, they likely play a role in temporal orienting to upcoming events (Schroeder and Lakatos, 2008). Theta-band activity, especially in the hippocampus, has been shown to serve a crucial function in working memory (Miller, 1991). Alpha-band activity (ABA) has been suggested to act as a local sensory gating mechanism, by which processing of relevant sensory inputs is enhanced and irrelevant input is suppressed (Foxe and Snyder, 2011). Additionally, an involvement of ABA in working memory has been reported (Klimesch et al., 2006). Modulations of BBA have frequently been described in the context of the preparation and execution of motor responses (Neuper et al., 2006), as well as during somatosensory processing (Kilavik et al., 2013). Recently, BBA has been suggested to also play a role in higher cognitive processing (Engel and Fries, 2010; Donner and Siegel, 2011). Lastly, gamma-band activity has been associated with a wide range of cognitive functions, like feature integration (Keil and Müller, 2010), object segregation (Castelo-Branco et al., 2000), selective attention (Fries et al., 2001; Kahlbrock et al., 2012) and multisensory processing (Senkowski et al., 2007).

Apart from a categorization into distinct frequency bands, neural oscillations are commonly classified as spontaneous or event-related (Makeig et al., 2004). Spontaneous activity is recorded from subjects during quiet wakefulness, without providing any task or external

stimulation. While long regarded as mere background noise, research in the past two decades has shown increasing interest in this sort of activity (Hanslmayr et al., 2007; Busch et al., 2009; Keil et al., 2013). The emerging notion of the brain is that of an active pattern generating system rather than a mere passive stimulus-driven information processing device (Singer, 2013). As such, the response of the brain to an incoming sensory stimulus is highly dependent on the brain's state prior to the occurrence of the stimulus. Recent studies have demonstrated the relevance of spontaneous prestimulus activity for perception (Busch et al., 2009) and motor related processing (Drewes and VanRullen, 2011). Event-related activity is observed following an external stimulus or a marked internal process, such as mental imagery or the initiation of a motor response (Luck, 2005). Event-related activity can be further divided into evoked (i.e. having a constant onset and a constant phase relation to the stimulus event) and induced activity (i.e. showing a significant latency and phase jitter; Makeig et al., 2004). There are numerous examples for the involvement of event-related, evoked and induced oscillations in cognitive tasks (e.g. Busch et al., 2006; Gruber et al., 2008; Naue et al., 2011). Taken together, oscillatory phenomena are readily observed in a wide range of neural processes. While, up to now, most research has focused on the role of single frequency bands, some attempts exist to establish a general framework on the functional significance of neural oscillations. I will discuss two of the most popular theories in this regard, i.e. 'communication through coherence' and 'binding by synchrony', in the following section.

2.3. 'Communication through coherence' and 'binding by synchrony'

Anatomical tracing studies in mammals demonstrate that neurons in the brain, especially in the cortex, constitute a highly interconnected complex hierarchical network (Buzsáki, 2006; Markov and Kennedy, 2013). Within this hardwired anatomical network, it is likely that a mechanism exists which creates transient functional connections in order to flexibly transfer information. In his communication through coherence theory, Fries (2005) proposed a framework, on how neural information processing could exploit oscillatory activity to flexibly select and route information at a fast timescale. As neural oscillations presumably reflect up and down shifts of postsynaptic potentials, they essentially serve as periodic variations in neuronal excitability (Bishop, 1933). In other words, neural oscillations likely reflect the

potential of the underlying neural population to receive and transmit information. According to Fries (2005) information can be routed between different areas by synchronizing their respective neural oscillations. As a result, this synchronization creates temporal windows for communication during which large volleys of action potentials at the sending site and a state of strong depolarization at the receiving site co-occur. At the same time, this mechanism suppresses information transfer to other, non-synchronized downstream neurons (e.g. in other brain areas). As neural assemblies can modify their state of synchronization at a time scale of milliseconds, this mechanism allows for the fast and flexible routing of information between different areas that is consistent with our everyday experience, that is, with our ability to rapidly shift our attention, update our goals, retrieve memories, and remap motor output. In the past years a growing number of studies have revealed empirical evidence for the important role of oscillatory activity in neural communication. For example, examining single neuron activity from the visual cortex of monkeys and cats, Womelsdorf et al. (2007) demonstrated that the correlation of gamma-band power between groups of neurons depends on their phase synchronization. The stronger the synchronization the stronger the mutual gamma power correlation, with changes in phase synchronization preceding changes in power by a few milliseconds. In another study, Colgin et al. (2009) provided compelling evidence for an involvement of oscillatory activity in the routing of information in the hippocampus. The authors showed that information transfer between CA1 and entorhinal cortex, as well as between CA1 and CA3 is mediated by fast (25 – 50 Hz) and slow (65 - 140 Hz) gamma oscillations, respectively. Moreover, the two rhythms were phase locked to the hippocampal theta rhythm, however, at different phase angles. Thus, the gamma band mediated transfer of information was related to oscillatory activity in the theta band. Demonstrating the influence of neural oscillations for motor behavior, Schoffelen et al. (2005) showed an increase in gamma-band coherence between neural activity in the contralateral motor cortex and electromyographic activity at the response hand during a cued speeded response task. Interestingly, this coherence varied as a function of target onset predictability, indicating a behaviorally relevant role of the observed coherence. Another possible function of neural oscillations, which is related and fully compatible with the communication through coherence framework by Fries (2005), is binding by synchrony (Engel and Singer, 2001). Binding by synchrony provides an elegant solution to the so-called 'binding problem', which comprises the fact that neural representations of objects, events or

goals involve processing in several distributed cortical networks. The binding by synchrony theory states that neural assemblies coding for one object synchronize their activity in the millisecond range, thereby forming a dynamic functional relationship (Gray, 1999). The results of numerous studies have provided evidence in support for this theory. For example, Kreiter and Singer (1996) recorded activity from spatially separated cells in the macaque middle temporal area. The authors found that the cells with overlapping receptive fields but different preferences for motion direction synchronized their activity when their receptive fields were stimulated with a single moving bar. Importantly, the cells did not synchronize their activity when each cell was stimulated with a separate bar, even when moved in the preferred direction. Castelo-Branco et al. (2000) reported a similar finding. In their study neurons in two separate areas of cat visual cortex synchronized their activity when coding for the same object, but not when coding for different objects. Along with many other studies (e.g., Gray et al., 1989; Engel et al., 1991; Neuenschwander and Singer, 1996) these findings demonstrate that neural synchrony between remote sites plays an important role in perceptual binding.

In summary, the frameworks of communication through coherence and binding by synchrony present promising integrative accounts on how information may be integrated and processed in the brain. While the two frameworks highlight different aspects of global neural information processing, they are fully compatible with each other and are both supported by empirical evidence (Fries, 2005).

3. Beta-band oscillations

3.1. Involvement in motor processes

Among the different frequency bands discussed above, the functional significance of beta band oscillations may be least understood (Engel and Fries, 2010). At the same time, interest in beta-band oscillations has recently undergone a major renaissance. Originally being interpreted primarily as a sensorimotor-related phenomenon, research now suggests additional important roles for this frequency band in selective attention and large scale neuronal integration (Engel and Fries, 2010; Donner and Siegel, 2011b). The earliest reports of BBA date back to the pioneering works in human electrophysiology by Berger (1931), Jasper and Andrews (1936), as well as Jasper and Penfield (1949). Initially suspected to be an epiphenomenon of metabolic activity (Berger 1931), it was soon found that BBA in sensorimotor areas is suppressed by somatosensory input (Jasper and Andrews, 1936). A few years later, Jasper and Penfield (1949) observed that BBA is also suppressed prior to and during on- and offset of a movement. These initial studies firmly tagged BBA as a sensorimotor rhythm, whose functional role has been investigated in a large number of experiments since then.

Depending on the experimental setup, a suppression of BBA is found that starts up to 1000 ms prior to movement onset. This BBA suppression likely originates in contralateral sensorimotor cortex (Stancák and Pfurtscheller, 1996; Doyle et al., 2005) and spreads to bilateral sensorimotor areas at movement onset (Neuper et al., 2006). Moreover, BBA suppression is sustained as long as the effector is moving (Wheaton et al., 2009) or as changes in muscle contraction appear (Omlor et al., 2011). Following the offset of a movement, a rebound of BBA is observed about 300 to 1000 ms post-movement, which probably originates from primary and supplementary motor areas (Kilavik et al., 2013). Functionally, some authors have proposed that the pre-movement BBA suppression reflects an activation or presetting of the sensorimotor network in anticipation of a movement (Pfurtscheller and Lopes Da Silva, 1999), including an increase in corticospinal excitability (Chen et al., 1998). The BBA rebound after movement offset has been interpreted as an active inhibition of motor areas (Solis-Escalante et al., 2012). For example, one study showed that transcranial magnetic stimulation (TMS) induces reduced motor excitability during the post-movement period (Chen et al., 1998). A further hypothesis posits that the post

movement BBA rebound is functionally distinct from the pre-movement suppression, and represents a recalibration of the motor network for subsequent movements (Kilavik et al., 2013). Interestingly, the modulation of sensorimotor BBA is also present during passive movement (Keinrath et al., 2006), as well as motor imagery (McFarland et al., 2000) and movement observation (Babiloni et al., 2002). Moreover, movement-related BBA is altered in persons with motor impairments (Leocani and Comi, 2006). In addition, transcranial alternate current stimulation (TACS) in the beta frequency range over sensorimotor areas leads to changes in motor output (Pogosyan et al., 2009). Together, these findings emphasize a functional role of BBA in the initiation of movements. The finding that BBA in sensorimotor areas synchronizes with electromyographical activity recorded at the effectors prior to and during a movement suggests that it may be directly involved in the descending transfer of motor commands (Baker et al., 1997). Thus, although important questions still remain unresolved, such as the relationship between pre- and post-movement modulations (Kilavik et al., 2013) the involvement of BBA in motor processing is firmly established.

3.2. Beyond motor functions:

As reported already by Jasper and Andrews (1936), BBA over sensorimotor areas can also be suppressed by somatosensory stimulation. This suppression, which has been replicated many times since, closely resembles that of ABA in primary visual areas following visual stimulation (Neuper and Pfurtscheller, 2001). Thus, it has been suggested that, similar to the functional role of ABA in the visual and other sensory modalities, BBA suppression plays a role in sensory gating in the somatosensory system (Neuper et al., 2006). Interestingly, BBA is not only suppressed by actual sensory stimulation, but also by the expectancy of a somatosensory input. For instance, Bauer et al. (2012) reported a suppression of BBA over somatosensory areas after participants were cued to attend to the tactile compared to when they were cued to attend to the visual modality. In a study on spatial attention by Van Ede et al. (2011), participants were cued to attend to either their left or right hand prior to the presentation of a tactile stimulus. The authors reported a spatial selective BBA reduction in somatosensory areas contralateral to the attended side. Likewise, in **Study 3** of the present thesis (Pomper et al., in preparation) we report a decrease in BBA over contralateral somatosensory areas and an increase of BBA in visual areas when participants attended

towards an upcoming tactile stimulus while ignoring a simultaneous visual input. Taken together, these results suggest a role of BBA not only in stimulus processing but also in anticipatory selective attention. Presumably, this attentional modulation is based on similar underlying mechanisms as alpha-band mediated visual attention, whereby a decrease of activity reflects a state of increased processing capabilities (Neuper et al., 2006).

Apart from tactile stimulation, it has been shown that nociceptive input modulates somatosensory BBA (Raij et al., 2004; Ploner et al., 2006; Pomper et al., 2013). For example, Ploner et al. (2006) reported a large-scale suppression of BBA following a painful stimulus, encompassing not only sensory but also motor regions. The authors suggested that this global impact underlines the biological significance of pain. Pain seems to demand widespread sensory attention and facilitate motor responses. In **Study 1** of this thesis (Pomper et al., 2013) we also found a bilateral suppression of sensorimotor BBA following painful electric stimuli to the left index finger. This suppression was stronger for high compared to low intensity pain stimuli. Interestingly, some recent studies suggested that also processing of stimuli from modalities other than somatosensation is reflected in changes in BBA. Mazaheri et al. (2014) reported an increase of BBA in auditory areas when subjects attended away from the auditory modality, supporting the role of BBA in sensory gating. Leske et al. (2013) found the strength of ABA and BBA in auditory cortex to be negatively correlated with the intensity of an auditory illusion. Similarly, in **Study 2** of the present thesis (Senkowski, Pomper et al., 2013), we found that poststimulus suppression of BBA was particularly involved during auditory processing in individuals with bilateral cochlear implants. Modulations in BBA were also found in the visual cortex. In an intersensory attention task, Bauer et al. (2012) found a stronger suppression of BBA over visual areas during visual attention than during tactile attention. Using a similar paradigm as Bauer et al., this aspect of attentional beta-band modulation was replicated in **Study 3** of the present thesis (Pomper et al., in preparation). While the above discussed examples suggest an overall involvement of BBA in attention and stimulus anticipation, an interesting recent hypothesis indicates a specific role for BBA in the temporal expectancy of upcoming stimuli (Arnal, 2012). Research has shown that, via the mechanism of so called 'temporal orienting', subjects are able to direct their attention to specific points in time, and thereby facilitate perception and processing of stimuli occurring at that moment (Miniussi et al., 1999; Rohenkohl et al., 2013; Sanabria and Correa, 2013). Recently, a number of studies have

ascribed this mechanism to BBA in motor areas (Arnal, 2012; Arnal and Giraud, 2012). For example, Saleh et al. (2010) found an entrainment of beta-band power fluctuations in primary motor cortex to the temporal properties of a series of cues. However, this was only the case when the cues were informative about the upcoming target. Fujioka et al. (2012) reported that suppression and rebound of BBA over sensorimotor areas reflects the temporal regularities of a stream of auditory clicks during passive listening. Furthermore, Cravo et al. (2011) reported an increased coupling of sensorimotor BBA power to the phase of delta oscillations after the omission of a temporally highly expected target. This suggests that sensorimotor BBA is involved in updating of temporal expectations. Notably, in **Study 3** of the present thesis (Pomper et al., in preparation), we also found that temporal orienting is reflected in BBA over sensorimotor areas, particularly contralateral to the hand that produces a motor response. Thus, BBA in sensorimotor areas seems to reflect temporal information relevant for the performance of a given task. This is especially the case in tasks featuring strong temporal regularities.

In summary, it is becoming increasingly clear that the modulation of BBA is not only associated with somatosensation, but also with visual and auditory processing. Similar as ABA, BBA seems to serve a sensory gating mechanism. It is likely that BBA is functionally significant for a wide range of cognitive operations, such as anticipatory attentional modulation, stimulus processing, and preparation and execution of motor output.

3.3. Beta-band oscillations in large-scale neural integration

The co-occurrence of BBA responses during both stimulus expectancy and processing, as well as motor preparation and execution may point to an integrative function of this frequency band. Indeed, a recent review suggests that BBA serves an important role in large scale neural communication (Donner and Siegel, 2011). In their framework, Donner and Siegel (2011) argue that fast gamma oscillations operate locally by encoding motor plans or perceptual representations. Integration of multiple local networks during processes such as decision making, multisensory integration, or the execution of motor programs, may be mediated by slower beta-band oscillations. Studies on perceptual ambiguities and illusions, which demand integrative processing of perception, sensory decision-making and subsequent motor responses, hint at such a role of BBA. For instance, Hipp et al. (2011)

identified a large-scale network in the beta band, whose specific connectivity determined the perception of a following ambiguous multisensory stimulus. Likewise, Keil et al. (2013) reported stronger BBA in left temporal gyrus, as well as an increased beta band-connectivity between left temporal gyrus and auditory areas preceding an auditory-visual illusion. With regard to these findings, it is conceivable that BBA subserves the integration of specific attentional task requirements, stimulus processing, and subsequent mapping of motor output. A similar functional relevance might underlie the BBA in some of the above discussed studies (e.g., Donner et al., 2009; Bauer et al., 2012; Pomper et al., 2013; Senkowski, Pomper et al., 2013.). A complementary account has recently been put forward by Engel and Fries (2010), who proposed a functional role of BBA in the maintenance of the current sensorimotor and cognitive state. The authors suggested that an expected change of state is accompanied by a decrease of BBA in relevant cortical areas. This putative decrease reflects the anticipation of behaviourally relevant events, and thus, a change from a passive to an active processing state.

To summarise, an increasing body of research suggests an involvement of BBA in a wide array of cognitive functions that goes beyond the realm of motor-related processing. Recently proposed theories on the role of BBA in large-scale neural communication or the maintenance of a current sensorimotor state represent interesting frameworks for an integrative view on BBA (Engel and Fries, 2010; Donner and Siegel, 2011). The three original studies of the present thesis emphasize this multifaceted involvement of BBA in cognitive processes. The studies demonstrate that BBA occurs during (i) multisensory processing of painful stimuli (Study 1), (ii) during auditory localization in individuals with bilateral cochlear implants (Study 2), and (iii) during a combined intersensory attention and temporal orienting task (Study 3).

4. Beta-band oscillations in multisensory perception and selective attention

4.1. Study 1: “Crossmodal bias of visual input on pain perception and pain-induced beta activity (Pomper et al. 2013)”

Research question:

Previous studies have shown that the perception and processing of acute pain is influenced by various other sensory input, most prominently by vision. Research on crossmodal integration of stimuli from modalities other than pain has demonstrated that the benefits of integration are strongest when the constituting unimodal stimuli are minimally effective in producing responses. This so called ‘principle of inverse effectiveness’ has to date not been studied for the integrative processing of pain. In **Study 1** we investigated inverse effectiveness at the behavioral and neural level for the multisensory processing of painful electric (i.e. intracutaneous stimuli) and visual stimuli (i.e. Gabor patches) of different stimulus intensities.

Results and discussion:

In line with the principle of inverse effectiveness, we found stronger crossmodal integration effects of visual input on subjective pain ratings for low compared to high intensity intracutaneous electric pain stimuli. Furthermore, we found stronger crossmodal interactions in right-central event-related potentials (ERPs, 150-200ms) for low compared to high intensity pain stimuli. Moreover, we observed inverse effectiveness in neural responses, reflected in enhanced suppression of medio-central BBA (12-24 Hz, 200-400ms) for low compared to high intensity pain stimuli presented with Gabor patches. Our findings suggest a facilitation of stimulus processing due to the additional presentation of a visual stimulus that serves to enhance response readiness of the sensorimotor system following painful stimulation. Overall, this study demonstrates that crossmodal integration between visual and pain stimuli follows the principle of inverse effectiveness and suggests a role for beta-band oscillations in the crossmodal modulation of pain.

4.2. Study 2: “Beta-band activity in auditory pathways reflects speech localization and recognition in bilateral cochlear implant users (Senkowski, Pomper et al. 2013)”

Research question:

Nowadays, a growing number of cochlear implant (CI) candidates receive bilateral implants, to utilize the benefits of binaural hearing. While speech comprehension in bilateral CI users is generally high, they demonstrate difficulties in localizing auditory speech, especially when localizing stimuli from the same hemifield. In normal hearing subjects, auditory stimulus localization comprises processing via a postero-dorsal pathway. Hence, a reason for the difficulties in stimulus localization in bilateral CI users could lie in a degeneration of this dorsal pathway, resulting from long periods of binaural deprivation prior to CI implantation. An alternative explanation is the limited temporal resolution of CIs, which might restrict the use of interaural time differences for stimulus localization. **Study 2** investigated this issue via source-localizing neural oscillations during auditory speech localization and discrimination in bilateral CI users and normal hearing controls.

Results and discussion:

In CI users, we found larger N1 amplitudes in the ERP during the localization compared to the recognition of auditory syllables. This suggests an enhanced stimulus processing effort in the localization task. Linear beamforming of oscillatory activity in CI users revealed stronger suppression of BBA after 200 ms in the postero-dorsal auditory pathway for the localization compared with the recognition task. In normal-hearing adults no effects were observed for N1 amplitudes or BBA. Our study suggests that stimulus localization requires more effort than stimulus discrimination for CI users. However, we could not find any evidence for a functional reorganization of cortical auditory pathways. Taken together, new signal processing strategies of cochlear devices preserving unambiguous binaural cues may improve auditory localization performance in bilateral CI users.

4.3. Study 3: “Anticipatory beta-band oscillations in sensorimotor cortex dissociate temporal orienting and intersensory visuo-tactile attention (Pomper et al., in preparation)”

Research question:

Intersensory attention describes our ability to selectively attend to one sensory modality, while ignoring inputs to other modalities. Temporal orienting refers to the ability to attend to specific points in time. Both processes have been shown to facilitate behavioral responses and modulate anticipatory neural oscillations in the alpha and beta band. Regardless of their common behavioral and neural correlates, these processes have been, thus far, studied widely independent of each other. In **Study 3** we used a two-by-two factorial design to investigate the interplay between intersensory attention and temporal orienting. We instructed participants to attend to either the visual or tactile modality (using an auditory cue), while presenting visuo-tactile target stimuli at either predictable or unpredictable times.

Results and discussion:

We found that frequency-specific modulations of neural oscillations at different locations reflect intersensory attention. While visual attention led to an increase of BBA in right somatosensory areas and a concurrent decrease of ABA and BBA in visual cortex, the opposite pattern was observed during tactile attention. Stronger activity of anticipatory BBA over sensorimotor areas, particularly contralateral to the response hand, reflected temporal orienting. Finally, we found no evidence for behavioral or neurophysiological interactions between intersensory attention and temporal orienting. Thus, despite their similar function and overlapping neural correlates, these processes may act independent of each other. We suggest that intersensory attention and temporal orienting are mediated by overlapping but widely independent and partly distinct neural oscillatory processes in the alpha and beta frequency ranges. These modulations likely reflect anticipatory attentional gating mechanisms that influence the processing of subsequently presented stimuli.

5. General discussion

5.1. Contribution of the present thesis

The three studies of my thesis show an involvement of beta-band oscillations in a wide array of tasks, including multisensory processing (**Studies 1 and 3**) and selective attention (**Studies 2 and 3**). In investigating a classic phenomenon of multisensory processing (i.e. inverse effectiveness), **Study 1** (Pomper et al., 2013) demonstrated a stronger suppression of BBA over sensorimotor areas in cases of stronger multisensory integration. In other words, simultaneous visual input modulates pain processing in sensorimotor areas. This finding provides further evidence for the notion that BBA plays an important role in large-scale neural integration and communication (Donner and Siegel, 2011). Furthermore, it extends the previous assumption that multisensory integration is primarily reflected in gamma-band oscillations (Senkowski et al., 2008). The BBA suppression following painful stimulation also matches with a recent framework that regards BBA as coding the current sensorimotor state (Engel and Fries, 2010). Painful stimuli are highly salient and often require a behavioral defense response. In line with this consideration, the pain-induced large-scale BBA suppression in **Study 1** supposedly reflects an instant and vital change of the sensorimotor state.

In combining aspects of multisensory processing and selective attention, **Study 3** (Pomper et al., in preparation) demonstrated an anticipatory modulation of BBA during an intersensory attention task. This task required a complex mapping between an instructional auditory cue and a visuo-tactile target, while implicitly modulating the participants' temporal expectancy. Hence, the paradigm requires processes of inter-areal neural communication and integration. In line with this assumption, we found the source-localized BBA at three separate cortical sites to each code for distinct aspects of the task. This finding further supports the notion that BBA plays an important role in large-scale inter-areal processing. Another finding of the study was that the specific strength of BBA modulation in sensory areas is significantly influenced by the attended sensory modality (visual vs. tactile). In this regard, **Study 3** extends previous findings by demonstrating a source-localized, spatially specific pattern of BBA modulation during selective visuo-tactile attention. It may be that this pattern relates to sensory gating mechanisms involving anticipatory attention modulations in ABA (Foxe and Snyder, 2011). The findings of Study 3 fit with the general

framework introduced by Engel and Fries (2010). The stronger local decrease of BBA in areas corresponding to the attended sensory modality can be seen as a change of the current sensorimotor state in anticipation of a behaviourally relevant target stimulus. As a further aspect of anticipatory selective attention, **Study 3** demonstrates the involvement of beta-band oscillations in temporal orienting. In line with the theory proposed by Arnal (2012) and adding to data from recent studies (e.g., Saleh et al., 2010; Fujioka et al., 2012), we found that BBA in bilateral sensorimotor areas, especially contralateral to the response hand, reflects predictability of target onset times. Importantly, **Study 3** extends previous literature on the function of BBA in selective attention by dissociating its role in intersensory attention and temporal orienting. At the same time, the finding of **Study 3** suggests simultaneous processing of separate task demands in two distinct BBA mediated networks.

Selective attention is also likely to underlie the BBA modulation observed in **Study 2** (Senkowski, Pomper et al., 2013). In patients with bilateral CI devices, medio-central BBA was stronger suppressed during auditory speech localization than during speech discrimination. This suppression might reflect increased processing demands in the postero-dorsal auditory pathway, which is known to mediate stimulus localization (Brunetti et al., 2005, 2008). Indeed, speech localization has been shown to be more demanding for bilateral CI users than for normal hearing control subjects (van Hoesel and Tyler, 2003; Litovsky et al., 2009), a finding which was also evident in the behavioral data from **Study 2**. Notably, the selective BBA suppression was still present when task difficulty was included as confounding variable in the statistical analysis. This suggests that the observed difference in BBA cannot be explained by task difficulty per se.

Taken together, the results of my thesis demonstrate that multisensory processing, which can be regarded as a prime example of inter-areal communication, involves modulations in beta-band oscillations. This is also the case for processing of pain, which is considered to induce widespread neural responses throughout the brain (Treede et al., 1999; Rainville, 2002). The modulation of BBA during auditory attention in **Study 2** is further evidence for the involvement of activity in this frequency band outside somatosensory processing. Finally, the data from **Study 3** crucially extend the findings of BBA during anticipatory selective attention by dissociating its role in intersensory attention and temporal orienting. Thus, recent studies as well as the findings of my dissertation provide strong evidence for the

notion of BBA as an important mechanism in higher cognition, well beyond sensorimotor processing.

5.2. Outlook and conclusion

Looking at the broad range of phenomena that have been associated with BBA, an important open question is whether a separation of BBA into functionally distinct sub-frequency bands might be appropriate. In this regard, future electrophysiological studies in humans and animals could aim at gathering more detailed information about the spectro-temporal characteristics, laminar profile, and cortical spatial origin of BBA. Related to this question is the possible association and interplay between beta- and alpha-band oscillations. As discussed in the previous sections, attention-related modulations of ABA and BBA are often observed in similar experimental paradigms. Specifically, a selective pattern of decrease and increase of power in areas corresponding to currently attended and unattended modalities, respectively, is well documented for both frequency bands (e.g. Foxe and Snyder 2011, Bauer et al. 2012). Thus far, it is unknown which parameters indicate the frequency range subserving this gating mechanism during selective attention. Likewise, the relationship between BBA and slow-wave oscillations in the delta band is currently not well understood. Several studies have reported a coupling of beta-band power to the phase of delta oscillations (Axmacher et al., 2010; Miskovic et al., 2011; Schutter and Knyazev, 2012). Also, both frequency bands are involved in temporal orienting towards upcoming events (Schroeder and Lakatos, 2008; Besle et al., 2011; Arnal, 2012; Fujioka et al., 2012). Whether delta- and beta-band oscillations code for different aspects of temporal expectancy, or whether temporal expectancy necessarily involves joint processing of both bands has not yet been addressed.

With the use of state-of-the-art EEG and MEG systems, as well as the development of more reliable source localizing approaches, the recent years have brought new confidence not only in EEG and MEG source analysis but also in the analysis of connectivity and directed connectivity (Baccalá and Sameshima, 2001; Gross et al., 2001; Siegel et al., 2012). These techniques seem promising for the functional investigation of large-scale networks and top-down selective attention. Moreover, by using non-invasive cortical stimulation techniques such as TMS and TACS, future studies could more directly target the functional significance of BBA and aim at uncovering causal relationships. For instance, the precise role of BBA in large-scale integration might be investigated by selectively disrupting parts of the network

using TMS (e.g. Groppa et al., 2013). Similarly, network functions could be investigated by enhancing present BBA via repetitive TMS and TACS (e.g. Pogosyan et al., 2009; Romei et al., 2011). Taken together, the combination of new theory-driven research and analysis approaches should guide future research, which will likely improve our understanding of the functional significance of neural oscillations in the brain.

In conclusion, neural oscillations are a fascinating phenomenon, whose proposed underlying function in neural communication and integration is both elegantly simple and yet overwhelmingly complex. Research has only begun to address the diverse mechanisms served by local as well as large scale oscillatory behavior and the specific role played by different frequency bands. While oscillations in the beta-band have traditionally been linked to motor behaviour and somatosensory processing, their implications in higher cognitive functions and large scale neural communication are now becoming increasingly evident. The three studies of my thesis contribute to a better understanding of beta-band oscillations in selective attention and multisensory processing, two highly complex and integrative functions. At the same time, these studies set the stage for a number of important outstanding questions and worthwhile goals for future research endeavours.

6. References

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7. Original Articles

7.1. Study 1

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7.3. Study 3

Pomper U., Keil J., Foxe J.J., Senkowski D. Intersensory selective attention and temporal orienting operate in parallel and are instantiated in spatially distinct sensory and motor cortices

Intersensory selective attention and temporal orienting operate in parallel and are instantiated in spatially distinct sensory and motor cortices

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Abstract

Knowledge about the sensory modality in which a forthcoming event might occur permits anticipatory intersensory attention. Information as to when exactly an event might occur enables temporal orienting. Intersensory and temporal attention mechanisms are often deployed simultaneously, but as yet it is unknown whether these processes operate interactively or in parallel. In this human EEG study we manipulated intersensory attention and temporal orienting in the same paradigm. A continuous stream of bisensory visuo-tactile inputs was presented, and a preceding auditory cue indicated to which modality participants should attend (visual or tactile). Temporal orienting was manipulated blockwise by presenting stimuli either at regular or irregular intervals. Using linear beamforming, we examined neural oscillations at virtual channels in sensory and motor cortices. Both attentional processes simultaneously modulated the power of anticipatory delta- and beta-band oscillations, as well as delta-band phase coherence. Modulations in sensory cortices reflected intersensory attention, suggesting a modality-specific gating mechanism. Modulations in motor and partly in somatosensory cortices reflected temporal orienting, indicative of a supramodal preparatory mechanism. Particularly, we found no evidence for interactions between intersensory attention and temporal orienting, demonstrating that these two mechanisms act in parallel and largely independent of each other in sensory and motor cortices.

Introduction

In navigating our environment, we typically confront continuous and varied input streams to our distinct sensory systems. Since we cannot reasonably process all these inputs to full elaboration, selective attention mechanisms such as intersensory attention and temporal orienting are deployed to focus our resources on inputs directly relevant to the task at hand. Intersensory attention describes our ability to attend to a specific sensory modality, while disregarding information from other modalities (Spence and Driver, 1997; Talsma et al., 2010). Temporal orienting of attention facilitates stimulus processing by reducing uncertainties about when an upcoming event will occur (Nobre et al., 2007; Arnal and Giraud, 2012). While both of these attention mechanisms can be deployed simultaneously, it is unknown whether they mutually influence each other or operate in an independent manner, and where in the cortical hierarchy they are instantiated.

Studies of intersensory selective attention have found shorter response times (RTs) when a relevant target is presented in the attended modality compared with when it is presented in the unattended modality (Spence and Driver, 1997; Mattler et al., 2006; Jong et al., 2010). A frequent finding in electrophysiological studies is a decrease of anticipatory occipital alpha-band activity (ABA, 8-12 Hz) when intersensory attention is drawn to the visual modality (Foxe et al., 1998; Fu et al., 2001). This decrease is paralleled by a simultaneous increase of ABA over cortical areas of unattended modalities, possibly reflecting an active sensory suppression mechanism (Foxe and Snyder, 2011, Gomez-Ramirez et al., 2011). Recent studies involving visual-tactile (Bauer et al., 2012) and auditory-tactile (van Ede et al., 2010) stimulation have shown similar modulations of beta-band activity (BBA, 13-30 Hz). Thus, amplification and suppression of ABA and BBA over sensory areas

likely reflect intersensory attention. Like intersensory attention, temporal orienting can facilitate RTs (Miniussi et al., 1999; Rohenkohl et al., 2012; Sanabria and Correa, 2013). Moreover, recent studies showed that temporal orienting modulates anticipatory BBA over sensory (Fujioka et al., 2012; Arnal et al., 2014) and motor areas (Saleh et al., 2010; Cravo et al., 2011; Fujioka et al., 2012). In addition, temporal orienting leads to a phase reset of slow-wave delta-band activity (DBA, 2-4 Hz) (Saleh et al., 2010; Besle et al., 2011; Cravo et al., 2013). Hence, temporal orienting is reflected in modulations of BBA and DBA. Taken together, intersensory attention and temporal orienting involve spectrally overlapping modulations of neural activity in sensory and motor cortices.

In this human electroencephalography (EEG) study, source localized oscillatory activity was examined in sensory and motor cortices during a visual-tactile cuing paradigm. Intersensory attention and temporal orienting were manipulated simultaneously, which enabled us (i) to dissociate the neural mechanisms underlying the two types of attention, and (ii) to examine whether they operate interactively or in an independent fashion. We found spatially distinct and modality-specific modulations of oscillatory power and phase coherence that differed between the two types of attention. Notably, we did not observe interactions between these mechanisms, suggesting that they operate in parallel, largely independently of each other, in spatially distinct sensory and motor cortices.

Methods

Participants

Twenty right-handed, paid volunteers participated in the study. Four participants had to be excluded due to extensive muscle or sweat artifacts in the EEG data. The remaining 16 participants (9 female, 23.2 years mean age) had normal or corrected to normal vision and reported no history of neurological or psychiatric illness. The study was conducted in accordance with the local Ethics Committee of the Charité – Universitätsmedizin Berlin as well as with the Declaration of Helsinki, and all participants provided written informed consent.

Setup and Procedure

Participants were seated in a dimly lit, electrically and acoustically shielded chamber, while being presented with visual, tactile, and auditory stimuli (Fig. 1). Prior to the main experiment, participants were presented with a passive localizer task (see below) and then performed two training blocks to familiarize themselves with the experimental paradigm. They were also informed that the stimuli were sometimes presented in a temporally regular and sometimes in an irregular fashion (Fig. 2a). This was done to ensure that all participants were aware of the possible regularity in the stimulus train. The experiment comprised of a two-by-two factorial design, with the factors ISI (regular or irregular) and Attention (attend-visual or attend-tactile) (Fig. 2b). At the beginning of each trial, an auditory cue was presented that indicated to which sensory modality participants should attend (attend-visual or attend-tactile). The auditory cue, which was delivered via in-ear air-pressure headphones (E-A-R tone Gold, Auditory Systems, Indianapolis, US), comprised of a sinusoidal 440 or 880

Hz tone with duration of 150 ms (including 5 ms rise and fall time). The mapping between the cue tone frequency and the attentional condition was counterbalanced across participants (e.g., in half of the subjects the 440 Hz tone instructed participants to attend to the visual modality). The cue was followed by an ISI, which blockwise had either a fixed (1700 ms) or variable (1000-2400 ms, mean 1700 ms) duration. Participants benefited from temporal orienting of attention especially when stimuli were presented with fixed ISIs. Following the ISI, a combined visuo-tactile stimulus was presented. Irrespective of the experimental condition, this stimulus randomly contained either a visual target (25 % of all trials), a tactile target (25 %), or no target (50 %; i.e. a standard; see below). The participants' task was to perform a speeded button press with the right index finger when a target was presented in the cued modality (e.g., they had to press the button to visual targets when attention was cued to the visual modality). No response was required for standards or for targets in the non-cued modality. Overall, participants were required to press a button on 25% of all trials. Following the stimulus, the cue of the next trial was presented either at a fixed interval of 1700 ms in the blocks with regular ISI or at a variable interval of 1000-2400 ms (mean 1700 ms) in blocks with irregular ISI. The main experiment comprised of 16 blocks lasting about 4 minutes each. In half of the blocks, stimuli were presented with fixed ISIs and in the other half with variable ISIs. Blocks with regular vs. irregular ISIs alternated after every second block. Each block consisted of 80 trials, half of which contained an attend-visual cue and the other half an attend-tactile cue (presented in random order). In total, 320 trials were presented for each of the four experimental conditions. Participants received visual feedback about the number of hits and misses, as well as on their mean RTs after each block.

Visuo-tactile Stimuli

All combined visuo-tactile stimuli were presented for 150 ms. Visual inputs were presented on a tilted TFT monitor at 40 cm distance from the eyes with a monochromatic neutral grey background (mean luminance of 30 cd/m²). Throughout experimental blocks, participants were instructed to focus on a central black fixation cross on the screen. In trials with standards and tactile targets, the visual input comprised of a centrally presented black and white Gabor patch with vertical gratings (diameter: 5.75°, spatial frequency= 1 cycle per degree, Gaussian standard deviation= 2°). In trials with visual targets the same Gabor patch was presented but it flickered at a frequency of 16.7 Hz. Tactile inputs were delivered to the index finger of the left hand by a 16-dot piezoelectric Braille display (4x4 quadratic matrix, 2.5 mm spacing; QuaeroSys, St. Johann, Germany). The Braille display was attached centrally to the backside of the TFT monitor so that it matched with the location of the visual inputs (Fig. 1). In trials with standards and visual targets, the tactile input comprised of a single elevation that lasted for 150 ms. In trials featuring tactile targets, all pins elevated and contracted at a frequency of 16.7 Hz. In order to mask the clicking noise by the Braille display during tactile stimulation, auditory white noise (150 ms duration) was presented via in-ear air-pressure headphones simultaneously with each visuo-tactile stimulus.

Localizer task

The reason for obtaining EEG data from a localizer task was to select regions of interest (ROIs) in sensory cortices for the analysis of neural oscillations in the main experiment (Fig. 3). The localizer task consisted of 120 unisensory visual and 120 unisensory tactile stimuli, which were presented blockwise at ISIs of 1300 ms. Visual stimuli were identical to the visual

components of the standards in the main experiment. Tactile stimuli were identical to the tactile components of the standards. To mask the noise by the Braille display, continuous white noise was presented via a battery-driven speaker throughout the entire localizer task. Participants were instructed to attend to the stimuli and to focus at a central fixation cross, but they did not perform a task. The use of a localizer task for the ROI selection had two major advantages: First, it allowed for ROI selection independent of the experimental manipulations in the main study. Second, stimuli in the main experiment comprised of simultaneously presented visual and tactile components, which hinders the source localization of the separate components.

EEG recordings and data preprocessing

EEG data were collected using a high-density 126-electrodes system (Easycap, Falk Minow services, Herrsching, Germany). To monitor eye movements, two additional electrodes were placed at the medial upper and lateral border of the right ocular orbit. Recordings were made against nose reference with a passband of 0.016–250 Hz and digitized at a sampling rate of 1000 Hz. All off-line data processing was done using Matlab (The MathWorks Inc., Natick, MA, USA), EEGLAB (<http://www.sccn.ucsd.edu/eeglab>; Delorme and Makeig, 2004) and FieldTrip (<http://www.ru.nl/fcdonders/fieldtrip>; Oostenveld et al., 2011). Data were off-line bandpass filtered (finite impulse response filter) between 0.3 and 125 Hz, downsampled to 500 Hz and re-referenced to common average. An additional narrow-band notch filter (49.8–50.2 Hz, 4th order two-pass Butterworth filter) was applied to remove line noise. Trials containing muscle and technical artifacts were removed by visual inspection. On average, 10.5 % of trials were removed. Electrodes with extremely high- and/or low-frequency artifacts throughout the recording ($M = 2.4$ $SD = 1.1$) were linearly interpolated using a

model of the amplitude topography at the unit sphere surface based on all nonartifactual electrodes (Perrin et al., 1989). To reduce artifacts such as eye-blinks, horizontal eye movements, electrocardiographic activity, as well as artifacts induced by the Braille display, an independent component analysis approach was applied (extended Runica, Lee et al., 1999). Components representing artifacts were removed from the EEG data by back-projecting all but these components (mean: 16.7; Schneider et al., 2008). Finally, continuous data were cut into epochs from -1500 ms to 1500 ms around cue onset for computing the baseline interval and around visuo-tactile stimulus onset for computing the analysis interval.

Analysis of oscillatory responses

For the analysis of oscillatory responses in the main experiment, we selected ROIs based on the findings from the localizer task. To this end, evoked responses from the unisensory-visual and unisensory-tactile stimuli of the localizer task were projected into source space using a linearly constrained minimum variance (LCMV) beamformer algorithm (Van Veen et al., 1997). This was done for a post-stimulus interval between 100 to 300 ms, with a -300 ms to -100 ms baseline. To compensate for potential rank reduction during preprocessing, the lambda regularization-parameter was set to 5%. Using these parameters, responses to unisensory-visual and unisensory-tactile stimuli were localized to the visual cortex and in the right somatosensory hand area, respectively (Fig. 3). Accordingly, two ROIs in the visual and right somatosensory hand areas were selected from the BrainMap database (Fox et al., 1994). An additional third ROI in the left motor cortex was selected. The reason for including this ROI was that activity in the left motor cortex reflects processes related to the preparation of a motor response (since participants responded to the target stimuli with the index finger of their right hand). In the next step of the analysis, a set of virtual electrodes

(Keil et al., 2014) corresponding to the ROIs was calculated from a three-dimensional grid covering the entire brain volume (resolution: 1 cm). The visual ROI comprised of 11 virtual electrodes, the right hand area of 4 electrodes, and the left motor area of 90 electrodes. To project raw data onto the virtual electrodes, they were multiplied with accordant spatial filters. This was done separately for each participant and grid point using a realistic three-shell boundary-element volume conduction model based on the MNI standard brain (MNI; <http://www.mni.mcgill.ca>). Using a LCMV beamformer (Van Veen et al., 1997) a common filter was constructed across all conditions from the covariance matrix of the averaged single trials at sensor level and the respective leadfield. The filter was calculated for an interval ranging from -700 to 700 and from -1200 to 200 ms around cue and visuo-tactile stimulus onset, respectively. The lambda regularization-parameter was set to 5%. Next, single trials were projected through these filters separately for each subject, condition, and virtual electrode. For the analysis of oscillatory power, the data at virtual electrodes were transformed into time–frequency domain by applying a sliding window Fourier transform with a single Hanning taper. Power at frequencies from 2 to 35 Hz was computed using a fixed time window ($t = 400$ ms) and a fixed frequency smoothing ($f = 1$ Hz). Total power was normalized relative to the pre-cue (-400 to -200 ms) baseline interval as follows:

$$Pow(t, f)_{normalized} = 100 \times \frac{Pow(t, f)_{poststimulus} - Pow(f)_{baseline}}{Pow(f)_{baseline}}$$

For the analysis of inter-trial phase coherence (ITC), we computed complex Fourier-spectra using sliding window Fourier transform with a single Hanning taper. In line with results from previous studies (Stefanics et al., 2010; Besle et al., 2011; Cravo et al., 2013), the analysis of phase coherence focused on slow-wave oscillations in the delta band. Fourier values at frequencies from 2 to 4 Hz were computed using a fixed time window ($t = 400$ ms) and a fixed frequency smoothing ($f = 1$ Hz). Complex Fourier spectra for each time point, frequency

and trial were amplitude-normalized by dividing them by their absolute values. ITC was then calculated as the mean normalized complex Fourier spectrum across trials.

Statistical analysis of behavioral data

Prior to the analysis, outlier trials with RTs above or below 3 standard deviations of the individual subject and condition mean were removed from the behavioral data. Mean RTs were then calculated for each participant and condition. To compare perceptual sensitivity between conditions, d' values were computed (Green and Swets, 1966) using the formula

$$d' = z(P(Y|s)) - z(P(Y|n)),$$

with $z(P(Y|s))$ being the z-score of the hit rate, and $z(P(Y|n))$ being the z-score of the false alarm rate. Because the z transform reaches infinity when percentages are equal to 0 or 100, datasets with values of 0 % and 100 % were assigned values of 1% and 99%, respectively (Macmillan and Creelman, 2005). Finally, RTs and d' values were compared between the experimental conditions using 2-way repeated measures ANOVAs with the factors ISI (regular vs. irregular) and Attention (attend-visual vs. attend-tactile).

Statistical analysis of neural oscillations

Time frequency power values were averaged across virtual electrodes separately for each of the three ROIs. In agreement with previous studies on intersensory attention (Foxe et al., 1998; Fu et al., 2001; Trenner et al., 2008; Bauer et al., 2012) and temporal orienting (Fujioka et al., 2009, 2012; Cravo et al., 2011, 2013) our analysis focused on effects in DBA, ABA and BBA. In the present study, neural oscillations were investigated in an interval ranging from -800 to -200 ms prior to the visuo-tactile stimulus. This interval was selected to avoid

temporal smearing of evoked activity by cue and stimulus onsets during time-frequency transformation. Across participants DBA, ABA and BBA were calculated as the mean power during selected interval separately for each condition and ROI. The power values were then submitted to 3-way repeated measures ANOVAs with the factors ISI (regular vs. irregular), Attention (attend-visual vs. attend-tactile), and ROI (visual ROI vs. somatosensory ROI vs. motor ROI). Significant interactions including the factor ROI were followed up by 2-way ANOVAs with the factors ISI and Attention, separately for each ROI. To examine effects in phase coherence between conditions, ITC values were subjected to a 3-way repeated measures ANOVAs with the factors ISI (regular vs. irregular), Attention (attend-visual vs. attend-tactile), and ROI (visual vs. somatosensory vs. motor). Significant interactions including the factor ROI were followed up by 2-way ANOVAs with the factors ISI and Attention, separately for each ROI.

Results

Behavioral data

Figure 2c illustrates RTs and d' values for the four experimental conditions. The 2-way ANOVA for RTs with the factors Attention (attend-visual vs. attend-tactile) and ISI (regular vs. irregular) revealed a significant main effect of ISI ($F_{(1,15)} = 19.03$, $p < 0.001$). Irrespective of the cued modality, RTs were shorter when stimuli were presented at regular compared with irregular ISIs. This shows that participants had a response advantage when stimuli were presented in a rhythmic fashion (i.e. with regular ISIs). No other significant main effects or interactions were found. Moreover, the 2-way ANOVA for d' value did not reveal any significant main effects or interactions. This suggests that the task difficulty was comparable across conditions.

Time-frequency representations of oscillatory power

The time-frequency analyses revealed power modulations in all three ROIs (Figs. 4-6). In the visual ROI (Fig. 4), an attend-tactile cue led to an increase in ABA, whereas an attend-visual cue caused a robust suppression in ABA. A similar pattern emerged in the delta and beta band, although there was no increase in DBA or BBA following the attend-visual cue. In the somatosensory ROI (i.e. contralateral to the tactile stimulation site), a robust suppression of BBA was observed (Fig. 5). The BBA suppression was stronger in the attend-tactile compared with the attend-visual condition. In addition, the BBA suppression was stronger in the irregular ISI compared with the regular ISI condition. Finally, in the motor ROI (i.e. contralateral to the response hand), a robust suppression of BBA was found (Fig. 6). The suppression was stronger in the irregular compared with the regular ISI condition. For the

statistical analysis, three-way ANOVAs with the factors ISI (regular vs. irregular), Attention (attend-visual vs. attend-tactile), and ROI (visual vs. somatosensory vs. motor) were calculated for each frequency band. Figure 7 provides an overview of the main statistical findings, which are described in detail in what follows.

Effects of intersensory attention and temporal orienting on oscillatory power

The ANOVA of DBA revealed a main effect for the factor ROI ($F_{(1,15)} = 46.94$, $p < 0.0001$). Although there was no significant interaction including the factor ROI, for exploratory purposes we conducted follow-up ANOVAs using the factors ISI and Attention, separately for each ROI. For the visual ROI, the ANOVA yielded a significant main effect of Attention ($F_{(1,15)} = 5.07$, $p < 0.04$), due to larger DBA in the attend-visual compared with the attend-tactile condition. At the motor ROI, the ANOVA yielded a robust main effect of ISI ($F_{(1,15)} = 16.72$, $p < 0.001$), due to larger DBA in the regular compared with the irregular condition. No significant effects were found at the somatosensory ROI. Thus, this analysis showed that temporal orienting and intersensory attention both modulate DBA amplitudes. Notably, the effects of these two types of attention were differentially reflected in the three ROIs. The three-way ANOVA of ABA revealed a significant main effect of Attention ($F_{(1,15)} = 9.09$, $p < 0.009$), due to stronger suppression of ABA in the attend-visual compared with the attend-tactile condition. Moreover, a significant interaction between Attention x ROI was found ($F_{(2,30)} = 22.51$, $p < 0.0001$). To further disentangle the effects of attention and ISI, planned follow-up 2-way ANOVAs with the factors ISI and Attention were calculated separately for the three ROIs. The ANOVA for the visual ROI yielded a significant main effect of Attention ($F_{(1,15)} = 28.8$, $p < 0.0001$), indicating that the suppression of ABA was larger in the attend-visual than in the attend-tactile condition. No other significant main effects or interactions were found

for the other ROIs and in relation to the factor ISI. The ANOVA of BBA revealed significant main effects of ROI ($F_{(2,30)} = 19.30$, $p < 0.0005$) and ISI ($F_{(1,15)} = 6.78$, $p < 0.0037$), indicating stronger BBA suppression in the irregular compared with the regular ISI condition. Furthermore, a significant interaction between Attention and ROI was found ($F_{(2,30)} = 16.64$, $p < 0.0001$). The follow-up 2-way ANOVAs for the visual ROI revealed a significant main effect of Attention ($F_{(1,15)} < 26.01$, $p < 0.0001$), due to a stronger suppression in the attend-visual compared with the attend-tactile condition. The follow-up ANOVA for the somatosensory ROI revealed a significant main effect of Attention ($F_{(1,15)} = 7.66$, $p < 0.014$), due to stronger suppression in the attend-tactile compared with the attend-visual condition, i.e. an effect in the opposite direction from the one found at the visual ROI. Furthermore, a significant main effect of ISI was observed ($F_{(1,15)} = 9.25$, $p < 0.0083$). In the somatosensory ROI, the suppression of BBA was stronger in the irregular compared with the regular ISI condition. Finally, the follow-up ANOVA for the motor ROI yielded a significant main effect of ISI ($F_{(1,15)} = 14.59$, $p < 0.0017$), indicating a stronger suppression of BBA power in the irregular compared with the regular ISI condition. Interestingly, no significant effects of intersensory attention were found in the motor ROI, suggesting that oscillatory activity in this region primarily reflects anticipatory processing of stimulus regularity.

Effects of intersensory attention and temporal orienting on inter-trial coherence

Fig. 8 illustrates ITC traces for the three ROIs. At the motor and the hand ROI, ITC was stronger for the regular compared with the irregular ISI condition. By contrast, no such difference was found at the visual ROI. The three-way ANOVA with the factors ISI, Attention, and ROI revealed a significant main effect for ISI ($F_{(1,15)} = 32.42$, $p < 0.001$). Across ROIs the ITC was stronger in the regular ISI compared with the irregular ISI condition. An additional

main effect of ROI was found ($F_{(1,30)} = 17.29$, $p < 0.001$), indicating stronger ITC in the somatosensory and motor ROI compared with the visual ROI. Although no significant interactions in relation to the factor ROI were observed, the traces illustrated on Fig. 8 indicate clear differences in ITC between the regular and irregular ISI conditions in the somatosensory and motor ROI but not in the visual ROI. For exploratory purposes, we calculated follow-up ANOVAs separately for the three ROIs. The ANOVAs for the somatosensory ROI yielded a significant main effect of ISI ($F_{(1,15)} = 18.42$, $p < 0.0007$), due to stronger phase coherence in the regular compared with the irregular ISI condition. Additionally, we found a significant main effect of Attention ($F_{(1,15)} = 5.24$, $p = 0.037$), indicating stronger ITC in the attend-tactile compared with the attend visual-condition. The follow up ANOVA at the motor ROI yielded a significant main effect of ISI ($F_{(1,15)} = 24.47$, $p < 0.0002$), due to stronger ITC in the regular compared with the irregular ISI condition. No other effects were found and no significant main effects or interactions were observed in the ANOVA for the visual ROI. Taken together, intersensory attention and temporal orienting seem to enhance ITC in the delta band, especially in the somatosensory cortex (effects of both types of attention) and motor cortex (effect of temporal orienting only).

Discussion

We investigated, for the first time, the simultaneous deployment of intersensory attention and temporal orienting within the same task. Temporal orienting during regular compared with irregular stimulation facilitated behavioral responses independent of the attended sensory modality. At the neuronal level, we observed distinct patterns of anticipatory DBA and BBA modulations in sensory and motor cortices, which differentially reflected the two attentional mechanisms. Notably, we found no evidence for interactions between the two processes, suggesting that they operate in parallel and in spatially distinct cortical substrates.

Temporal orienting facilitates behavioral responses to visual and tactile targets

Independent of the cued sensory modality faster RTs were recorded when stimuli were presented in a regular compared with an irregular fashion. This finding is in line with previous studies, which showed that temporal predictability in stimulus trains facilitates target processing (Zahn and Rosenthal, 1966; Coull and Nobre, 1998; Cravo et al., 2011). Participants in our study were not explicitly instructed to pay attention to the temporal regularities in the stimulus trains. However, they undoubtedly automatically oriented their attention to the expected target onset. Interestingly, we did not find interactions between the cued modality and temporal predictability. Previous studies have suggested the existence of a supramodal temporal orienting mechanism that facilitates behavioral responses independent of the sensory modality (Bolger et al., 2013; Lunghi et al., 2014). Hence, a supramodal temporal orienting mechanism may have contributed to the response time facilitation effects on visual and tactile targets in the present study.

Broadband neural oscillations in sensory cortices reflect intersensory attention

In the visual cortex we found a decrease of ABA when the visual modality was attended and an increase of ABA when the tactile modality was attended. Our source-space findings are in line with and extend previous reports of anticipatory ABA modulations by attention at the scalp level (Foxe et al., 1998; Foxe and Snyder, 2011; Bauer et al., 2012). The modulation in ABA has been attributed to a sensory gating mechanism, by which task irrelevant inputs are suppressed and task relevant inputs are enhanced (Lopes da Silva, 1991; Kelly et al., 2006). Interestingly, we also found a stronger suppression of BBA in visual regions when attention was directed to the visual modality. Comparable intersensory attention effects have been found for tactile (Bauer et al., 2012; van Ede et al., 2013) and auditory stimuli (Leske et al., 2013; Mazaheri et al., 2014). Hence, our findings suggest that anticipatory BBA modulations may serve a similar sensory gating mechanism as proposed for ABA. Finally, we observed a weak albeit significant effect in DBA, which was more strongly suppressed during visual compared with tactile attention. Thus, the effects of intersensory attention in visual cortex were reflected by a stronger anticipatory reduction in broadband oscillatory power when participants attended to the visual compared to the tactile modality (Fig. 4). In the somatosensory cortex, effects of intersensory attention were observed specifically in BBA. The suppression of BBA was stronger when participants attended to the tactile compared to the visual modality. Our source-space data fit with a number of recent MEG studies examining BBA at the sensor level (Ede et al., 2010; Bauer et al., 2012; van Ede et al., 2013). Bauer et al. (2012) reported a suppression of BBA over somatosensory areas when participants were cued to the tactile compared to the visual modality. Thus, our findings of anticipatory BBA modulations in the somatosensory cortex provide further

evidence that BBA may reflect an intersensory gating mechanism. Another finding was that delta-band ITC was stronger when participants attended to tactile compared to visual stimuli. The stronger ITC could reflect a phase reset of slow-wave oscillatory activity, which serves as an additional attentional selection mechanism (Schroeder and Lakatos, 2008; Gomez-Ramirez et al., 2011). In contrast to the sensory cortices, we did not find effects of intersensory attention in the motor cortex. This observation likely relates to the fact that go-targets in both modalities required the same motor response.

DBA and BBA in motor and somatosensory cortex reflect temporal orienting

Unlike intersensory attention, temporal orienting did not modulate anticipatory activity in the visual cortex. At first glance, this finding is in contrast with recent studies that showed entrainment effects of DBA (Cravo et al., 2013) and modulations of single neuron activity (Sharma et al., 2014) in visual areas during temporal orienting. A reason for this discrepancy could be that our task was relatively easy ($d' > 4$). Previous studies reporting temporal orienting effects in the visual cortex were more demanding (Correa et al., 2006; Cravo et al., 2013). In the somatosensory cortex we observed a stronger suppression of BBA when stimuli were presented in an irregular compared with a regular fashion. This finding is in line with recent electrophysiological studies that showed anticipatory modulations of BBA over sensory and motor areas during temporal orienting (Saleh et al., 2010; Cravo et al., 2011; Fujioka et al., 2012; Arnal, 2014; see Arnal, 2012 for a review). Another main finding was that the ITC of DBA was stronger during the regular compared with the irregular condition. Increased ITC could be a marker for an attention selection mechanism that entrains the phase of ongoing slow-wave oscillations so that the expected stimulus arrives at a state of high neuronal excitability (Schroeder and Lakatos, 2008). Electrophysiological studies in

humans have provided evidence for such a mechanism in sensory (Besle et al., 2011; Gomez-ramirez et al., 2011; Cravo et al., 2013) and motor areas (Saleh et al., 2010; Besle et al., 2011). In the motor cortex, temporal orienting was reflected by a similar pattern as in the somatosensory cortex: BBA was more strongly suppressed when stimuli were presented in an irregular compared with a regular fashion. It is well known that suppression of BBA relates to response preparation (Pfurtscheller, 1981; Kilavik et al., 2013). Accordingly, in this study, the stronger BBA suppression in the irregular condition likely reflects enhanced engagement of motor areas. By contrast, knowledge about the temporal onset of stimuli in the regular condition results in a less energy-demanding state, as reflected by reduced suppression of BBA. Finally, we observed an increase in power and ITC of DBA in motor cortex. As in the somatosensory cortex, we suggest that this reflects entrainment of DBA to the temporal properties of the stimulation. We would like to emphasize that the difference between regular and irregular conditions was much stronger in the motor than in the somatosensory cortex. This supports the recently proposed crucial role of neural oscillations in motor areas in temporal orienting (Arnal, 2012; Arnal et al., 2014).

Intersensory attention and temporal orienting operate independently in sensory and motor cortex

The analysis of neural oscillations in the different ROIs and frequency bands did not reveal significant interactions between the two types of attention. Although null results should be interpreted cautiously, we suggest that the complete absence of interactions indicates that intersensory attention and temporal orienting operate, to a substantial degree, independently of each other in separate sensory and motor cortices. This interpretation is supported by the behavioral results, which show that temporal orienting operates similarly

for visual and tactile stimuli. Moreover, the lack of interactions is in line with studies that suggest the existence of a supramodal temporal orienting mechanism (Lange and Röder, 2006; Bolger et al., 2013; Lunghi et al., 2014). However, other studies revealed that another attentional mechanism, namely spatial attention, interacts with intersensory attention (van Ede et al., 2010; Banerjee et al., 2011; Bauer et al., 2012). Banerjee et al. (2011) showed that, while both auditory and visual spatial attention modulate ABA, this modulation clearly shows a modality-specific topographical distribution. Further, spatial attention and intersensory attention both involve modulations of ABA and BBA in sensory areas (Bauer et al., 2012), which might facilitate interactions between these mechanisms. By contrast, temporal orienting also involves modulations of slow-wave DBA (Saleh et al., 2010; Besle et al., 2011; Cravo et al., 2013), which often operates on a global brain-wide scale (Buzsáki, 2006). This could be one reason why we did not find interactions between temporal orienting and intersensory attention in sensory and motor cortices. Whether these two mechanisms of attention interact in other cortical areas, such as prefrontal cortex, remains to be elucidated.

Conclusion

We investigated intersensory visuo-tactile attention and temporal orienting in the same experimental paradigm. We found that a combination of anticipatory BBA power and DBA power and phase modulations reflects both attention mechanisms. Effects of intersensory attention were observed in visual and somatosensory cortex, whereas effects of temporal orienting were found in motor areas and somatosensory cortex. Our data show that oscillatory responses in the delta and alpha band simultaneously encode separate attentional task demands. Despite their similar function and partially overlapping neural

signatures, we found no interactions between intersensory attention and temporal orienting. This study provides compelling evidence that spectrally and anatomically distinct patterns of neuronal activity encode intersensory attention and temporal orienting in a largely independent manner.

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Figure Legends

Figure 1. Experimental setup. Visual (Gabor-patches) and tactile (Braille) stimuli were presented simultaneously and spatially aligned. Participants placed their left hand palm-upwards on a board beneath a tilted TFT-monitor on which visual stimuli were presented. They touched the Braille-display with the tip of their left index finger. Behavioral responses to validly cued targets were made with the right index finger.

Figure 2. Illustration of the different experimental conditions and behavioral data. **a**, Stimulus train in the regular (upper timeline) and irregular (lower timeline) ISI condition. Auditory cues were followed by an ISI of regular or irregular duration. Following the ISI, a visuo-tactile stimulus was presented. This stimulus was always bisensory but was either constituting a visual target, a tactile target, or a standard. Participants were instructed to respond with a button press only if a target appeared in the cued modality. The focus of the EEG data analysis was on the interval preceding the visuo-tactile stimulus. **b**, Illustration of the 2 x 2 factorial study design. **c**, Mean reaction times (left barplot) and d' values (right barplot) for all four conditions.

Figure 3. Source localized responses to unisensory tactile (top) and unisensory visual (bottom) stimuli in the localizer task.

Figure 4. Power of neural oscillations in the visual ROI. **a**, Time-frequency representations of virtual electrodes for the visual (left panel) and tactile attention conditions (middle panel), and their difference (right panel), for the regular ISI condition (top row), the irregular ISI condition (middle row), and their difference (bottom row). The bottom right panel illustrates the location of the visual ROI in source space. **b**, Mean power change (-800 to -200 ms,

relative to baseline) for BBA (13-30 Hz), ABA (8-12 Hz), and DBA (2-4 Hz). Effects of temporal orienting are highlighted in ocher and effects of intersensory attention are highlighted in blue.

Figure 5. Power of neural oscillations in the somatosensory ROI. **a**, Time-frequency representations of virtual electrodes for the visual (left panel) and tactile attention conditions (middle panel), and their difference (right panel), for the regular ISI condition (top row), the irregular ISI condition (middle row), and their difference (bottom row). The bottom right panel illustrates the location of the somatosensory ROI in source space. **b**, Mean power change for BBA, ABA, and DBA. Effects of temporal orienting are highlighted in ocher and effects of intersensory attention are highlighted in blue.

Figure 6. Power of neural oscillations in the motor ROI. **a**, Time-frequency representations of virtual electrodes for the visual (left panel) and tactile attention conditions (middle panel), and their difference (right panel), for the regular ISI condition (top row), the irregular ISI condition (middle row), and their difference (bottom row). The bottom right panel illustrates the location of the motor ROI in source space. **b**, Mean power change for BBA, ABA, and DBA. Effects of temporal orienting are highlighted in ocher and effects of intersensory attention are highlighted in blue.

Figure 7. Overview of statistically significant findings.

Figure 8. Experimental effects on inter-trial coherence. Delta-band (2-4 Hz) inter-trial coherence during the prestimulus interval for the attend visual (top row) and attend tactile (bottom row) conditions at the motor (left column), hand (middle column) and visual ROI (right column).

Figure 1

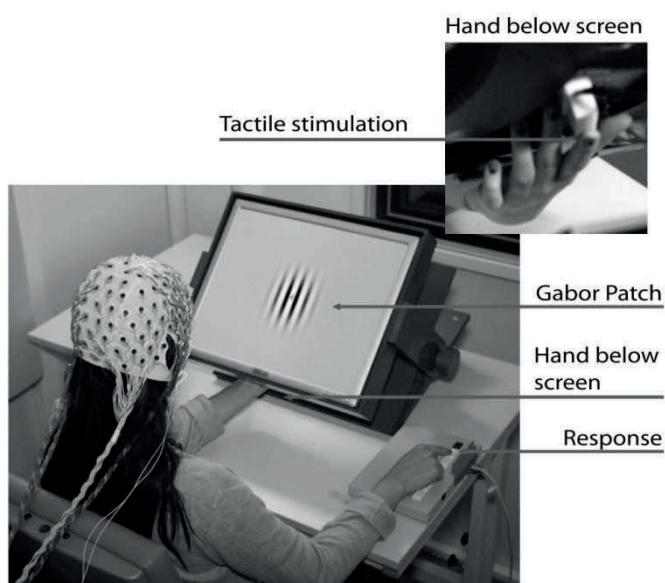


Figure 2

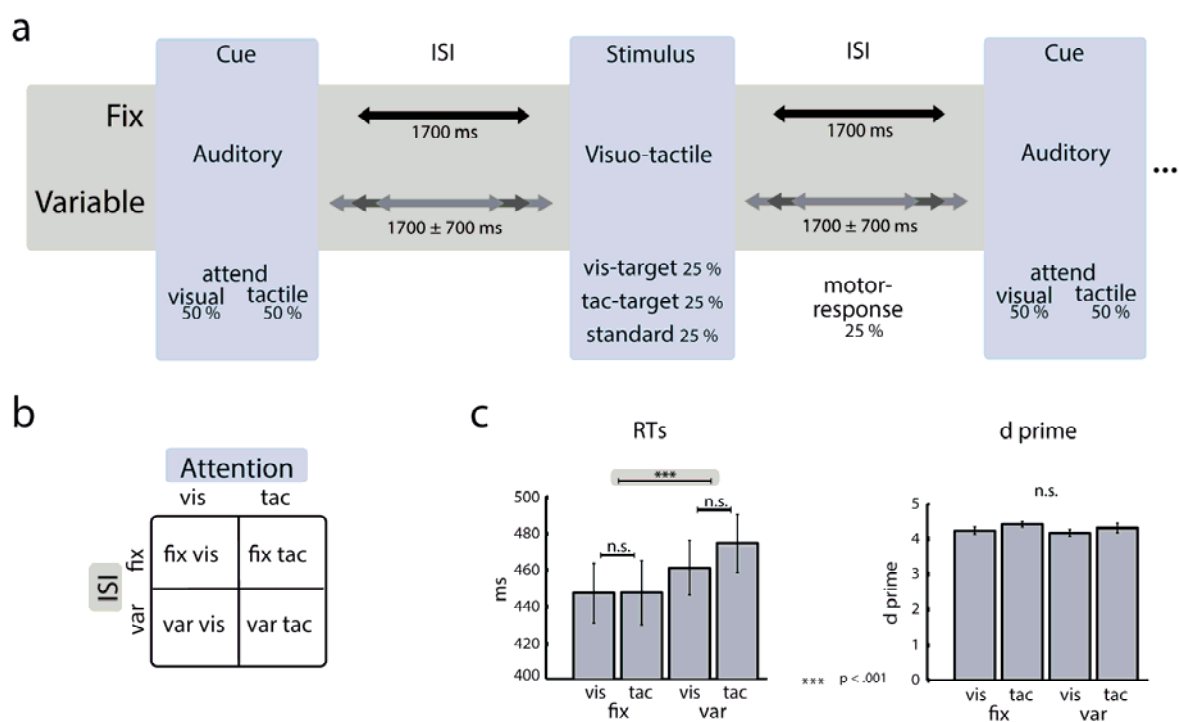


Figure 3

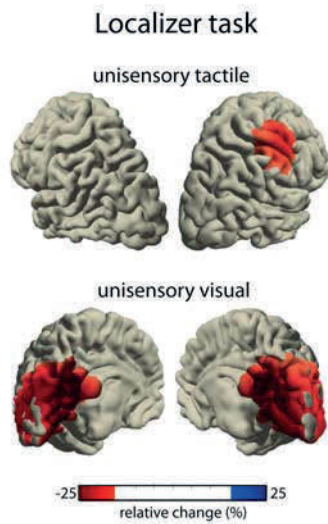


Figure 4

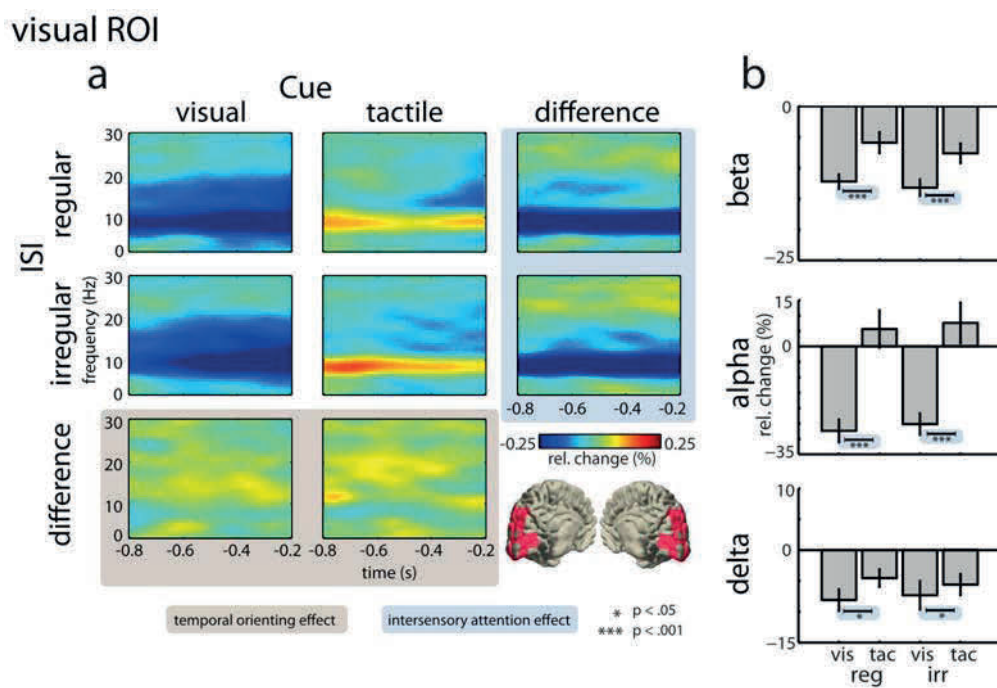


Figure 5

Somatosensory ROI

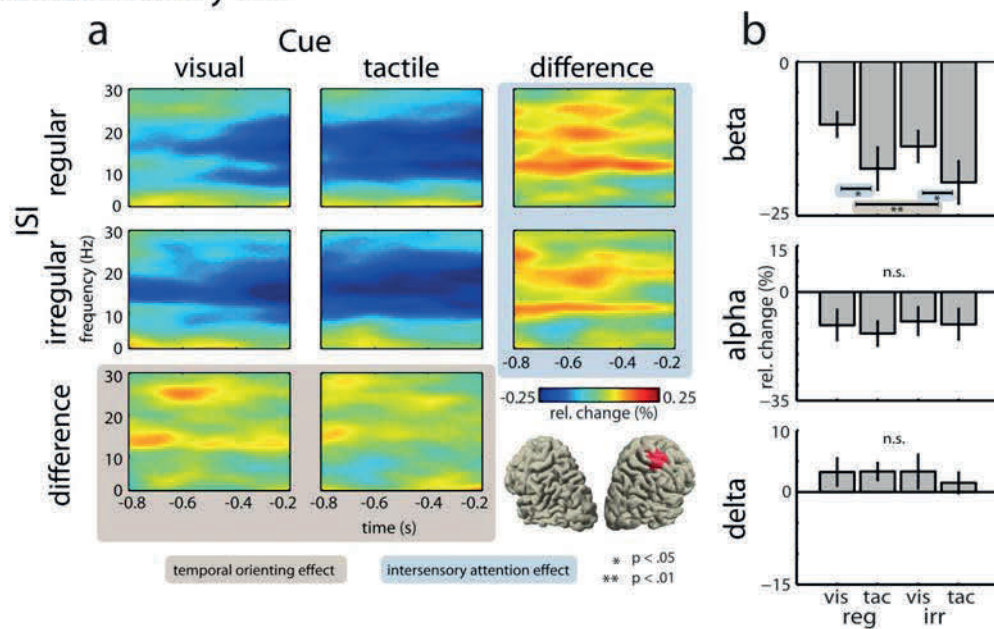


Figure 6

Motor ROI

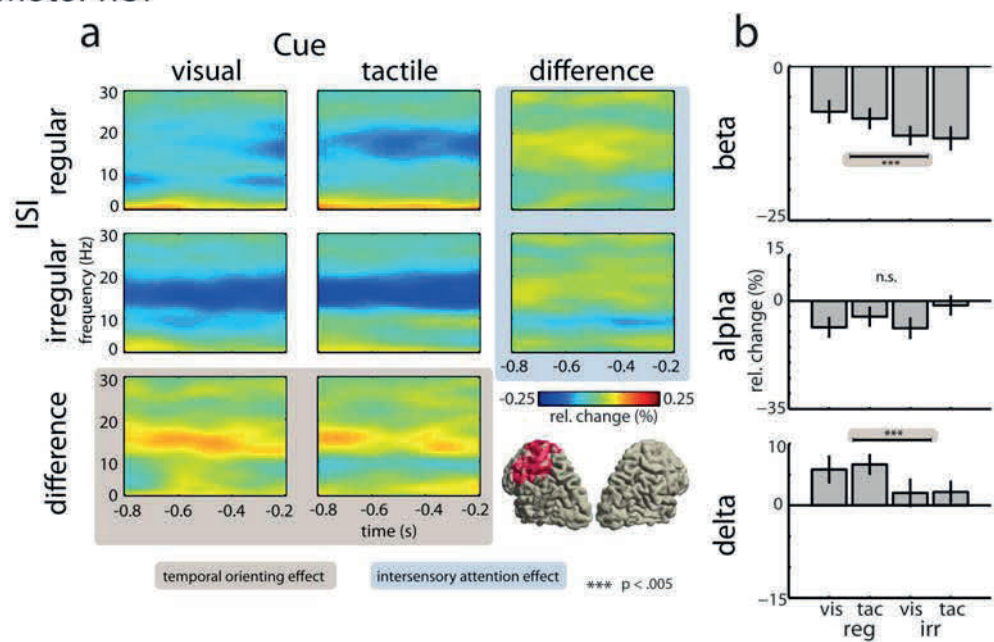
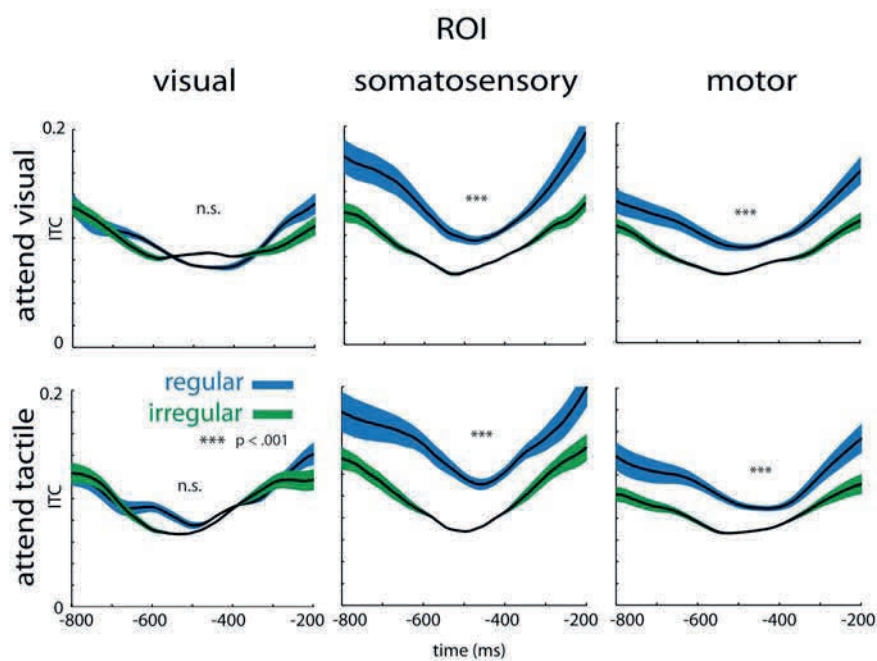


Figure 7

| ROI | | | | |
|------------------------|--------|---------------|-------|----|
| | visual | somatosensory | motor | |
| Beta | IA | IA | TO | TO |
| Alpha | IA | | | |
| Delta | IA | | | TO |
| ITC _(Delta) | | IA | TO | TO |

temporal orienting intersensory attention

Figure 8



8.Appendix: Publikationsliste, Danksagung, Eidesstattliche Selbständigkeitserklärung

Veröffentlichungen in Peer-Reviewed Zeitschriften:

Pomper U, Brincker J, Harwood J, Prihodko I, Senkowski D (2014). Taking a call is facilitated by the multisensory processing of smartphone vibrations, sounds, and flashes. *Plos One* 9:e103238

Höfle M, **Pomper U**, Hauck M, Engel AK, Senkowski D. (2013). Spectral signatures of viewing a needle approaching one's body when anticipating pain. *Eur J Neurosci.*, doi: 10.1111/ejn.12304

Senkowski D*, **Pomper U***, Fitzner I, Engel AK, Kral A. (2013). Beta-band activity in auditory pathways reflects speech localization and recognition in bilateral cochlear implant users. *Hum Brain Mapp.* 2013, doi: 10.1002/hbm.22388 *Shared first authorship

Pomper U, Höfle M, Hauck M, Kathmann N, Engel AK, Senkowski D. (2013). Crossmodal bias of visual input on pain perception and pain-induced beta activity. *Neuroimage*, 66, 469–478.

Mathes B, **Pomper U**, Walla P, Basar-Eroglu C. (2010). Dissociation of reversal- and motor-related delta- and alpha-band responses during visual multistable perception. *Neurosci Lett.*, 478(1):14-8.

Veröffentlichungen in Vorbereitung:

Pomper U., Keil J., Foxe J.J., Senkowski D. Intersensory selective attention and temporal orienting operate in parallel and are instantiated in spatially distinct sensory and motor cortices.

Poster und Vorträge:

Pomper U, Senkowski D, Fitzner I, Engel AK, Kral A. (2013). Beta-band activity in auditory pathways reflects speech localization and recognition in bilateral cochlear implant users. Poster at the 55rd Conference of Experimental Psychologists (TeaP)

Pomper U, Höfle M, Hauck M, Engel AK, Senkowski D. (2012) Spectral signatures of viewing a needle approaching one's body when anticipating pain. Talk at the 11th Charité Conference on Psychiatric Research

Pomper U, Höfle M, Hauck M, Engel AK, Senkowski D. (2011). Crossmodal biasing of pain: How visual stimulus intensity influences perception and processing of pain. Poster at the 2011 Neuroscience Meeting (SFN)

Pomper U, Höfle M, Hauck M, Engel AK, Senkowski D. (2011). Crossmodal biasing of pain: How visual stimulus intensity influences perception and processing of pain. Talk at the 53rd Conference of Experimental Psychologists (TeaP)

Pomper U, Höfle M, Hauck M, Engel AK, Senkowski D. Cross-modal interactions between visual and painful stimuli: A case of inverse effectiveness? (2010). Poster at the 11th International Multisensory Research Forum (IMRF)

Pomper U, Mathes B, Walla P, Basar-Eroglu C. (2008). Dissociating Perceptual from Motor Processes in Multistable Perception. Poster at the Xth International Conference on Cognitive Neuroscience (ICON)

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Selbständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Arbeit ohne unzulässige Hilfe und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe. Die aus fremden Quellen direkt oder indirekt übernommenen Gedanken habe ich als solche kenntlich gemacht.

Ort, Datum

Unterschrift